

CHAPTER 9: PATTERNS OF MACROFUNGI DIVERSITY

RESULTS

Patterns of Macrofungi Alpha Diversity

General Patterns

Fifty-five macrofungi genera were observed (Appendix 11), of which 25 were lichen, and the remainder were fleshy fungi. Macrofungi richness (fleshy fungi and lichen combined) per reach ranged from 0 to 16 ($\bar{x} = 7.25$, $SE = 0.45$). Taxonomic richness of macrofungi, including all unique taxa of macrofungi observed per reach, ranged from 0 to 19 ($\bar{x} = 8.92$, $SE = 0.52$). Taxonomic richness and genera richness were highly correlated ($r = 0.961$, $P < 0.001$). Genera richness was used to represent the diversity of all macrofungi because it facilitated the identification of specific taxa.

Ten macrofungi occurred on over 25% of all reaches ($n > 20$), with the 7 most frequent macrofungi being lichens (Fig. 62). The 10 most frequent macrofungi were responsible for over 60% of the macrofungi observations. *Letharia*, a fruitcake lichen which grows on tree bark, was the most frequent genus, occurring on approximately 80% of all reaches. *Rhizocarpon* is a crustose lichen known as “map lichen” that grows on rock substrates. The next 3 most frequent macrofungi were also crustose lichen. Two foliose lichen followed; *Umbilicaria* attaches to rocks and *Phycia* attaches to rocks or trees. The last 3 of the 10 most frequent macrofungi were fleshy fungi, including *Hemitrichia*, *Cryptoporus*, and *Polypore*. All of these macrofungi are forest associates, with *Hemitrichia* associated with downed logs, and *Cryptoporus* and *Polypore* belonging to the same family (Polyporaceae) and associated with dead and dying conifer trees. These 10 most frequent macrofungi constituted over 60% of all macrofungi observations, with the remaining 44 genera each having frequencies of occurrence of $\leq 25\%$ of all reaches.

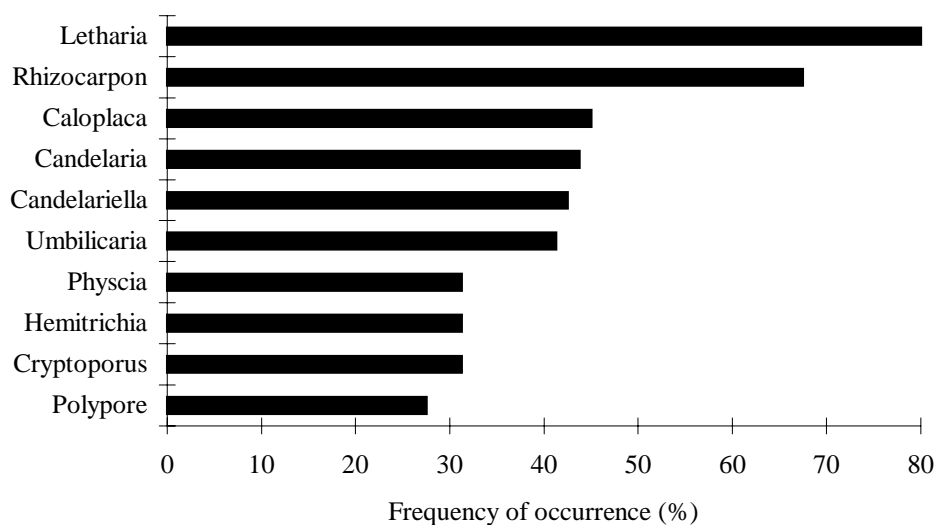


FIG. 60. Frequency of occurrence of 10 most frequent macrofungi. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of All Macrofungi

Regression Model for Macrofungi Richness

The richness of all macrofungi genera was correlated with 10 variables (Table 151). Regression models reflected correlations (Table 152). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel variables resulted in a one-variable model: a positive association with channel gradient (adj. $R^2 = 0.273$). Regression on vegetation variables resulted in a 4-variable model: positive associations with subalpine conifer, shrubs, canopy cover index, and large snags (adj. $R^2 = 0.343$). Backwards step-wise regression on these 5 key variables resulted a moderately strong 3-variable model, where macrofungi richness increased with increases in channel gradient, canopy cover index, and large logs (adj. $R^2 = 0.385$, Tables 152 and 153). No potential thresholds were observed by examining bivariate relationships between macrofungi richness and variables in the final model.

TABLE 151. Significant correlations ($P \geq 0.10$) between macrofungi richness and 22 environmental variables. Bolded values indicate $P \leq 0.05$. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Macrofungi richness	
	r	P
<i>Channel characteristics:</i>		
Gradient	0.531	<0.001
<i>Vegetation characteristics:</i>		
Meadow	-0.414	<0.001
Mixed conifer	0.189	0.092
Lodgepole pine	-0.204	0.070
Subalpine conifer	0.222	0.048
Canopy cover index	0.394	<0.001
Large snag	0.468	<0.001
Small snag	0.314	0.005
Small log	0.289	0.009
Large log	0.468	<0.001

TABLE 152. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and macrofungi genera richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Macrofungi richness
<i>Channel characteristics:</i>	
Gradient	P
<i>Vegetation characteristics:</i>	
Subalpine conifer	P
Canopy cover index	P
Shrub	P
Large snag	P
<i>Variables in final model</i>	
adj. R^2	0.385

TABLE 153. Final regression model of key environmental variables related to macrofungi genera richness. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Gradient	2.045	0.554	0.367	3.689	<0.001
Large snags	1.471	0.436	0.315	3.372	0.001
Canopy cover index	0.026	0.015	0.168	1.726	0.089

Macrofungi Richness by Basin Orientation

Macrofungi genera richness did not vary significantly by basin orientation (ANOVA, $P = 0.583$).

Macrofungi Richness by Environmental Gradients

Macrofungi genera richness showed numerous correlations with the 7 environmental gradients defined by principal components analysis (see Environmental Characteristics section above) (Table 154). Macrofungi genera richness was positively correlated with the elevation–precipitation and snag and log gradients. Alternatively, macrofungi richness was negatively correlated with the channel flow and forest to meadow gradients.

TABLE 154. Correlations between macrofungi genera richness and 7 environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.10$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradients	Macrofungi genera richness	
	r	P
<i>Physical gradient:</i>		
1. Elevation–precipitation	0.201	0.074
2. Channel flow	-0.346	0.002
<i>Vegetation gradient:</i>		
1. Forest to meadow	-0.365	0.001
2. Subalpine vegetation	0.155	0.171
3. Alder–willow	-0.062	0.586
4. Aspen–cottonwood	-0.165	0.143
<i>Woody debris gradient:</i>		
1. Snag and log	0.475	<0.001

Patterns of Lichen and Fleshy Fungi Diversity

General Patterns

Macrofungi includes both lichen and fleshy fungi. Lichen and fleshy fungi are associated with divergent substrates, and are likely to respond to environmental conditions differently. These two taxonomic groups of fungi were analyzed separately to describe their environmental relationships.

A total of 30 fleshy fungi genera and 25 lichen genera were encountered during sampling. Fleshy fungi were detected on 45% ($n = 36$) of the reaches. The average frequency of occurrence for fleshy fungi was 5.0 (SE = 1.28), and their richness ranged from 0 to 10 ($\bar{x} = 1.89$, SE = 0.32) genera per reach. Lichen were detected on 88.8% ($n = 71$) of the reaches. The average frequency of occurrence for lichen was 17.2 (SE = 3.47), and their richness ranged from 0 to 13 ($\bar{x} = 5.36$, SE = 0.38) genera per reach. The richness of lichen and fleshy fungi genera were negatively correlated, but not significantly ($r = -0.177$, $P = 0.116$).

Environmental Relationships of Lichen Richness

Regression Model for Lichen Richness

Lichen richness was correlated with 7 environmental variables (Table 155). Regression models reflected correlations (Table 156). Regression on abiotic environmental variables resulted in no variable being selected. Regression on channel variables resulted in a one-variable model: a positive association with channel gradient (adj. $R^2 = 0.122$). Regression on vegetation variables resulted in a 3-variable model: positive associations with subalpine conifer, canopy cover index, and large snags (adj. $R^2 = 0.302$). Backwards step-wise regression on these 4 key variables resulted in the vegetation model, where lichen richness increased with increases in subalpine conifer, canopy cover index, and large snags (adj. $R^2 = 0.302$) (Tables 156 and 157)

TABLE 155. Significant correlations ($P \geq 0.10$) between the richness of 2 macrofungi groups and 22 environmental variables. Bolded values indicate $P \leq 0.05$. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Lichen richness		Fleshy fungi richness	
	r	P	r	P
<i>Channel characteristics:</i>				
Gradient	0.365	0.004	0.331	0.003
<i>Vegetation characteristics:</i>				
Meadow	-0.416	<0.001	N	n.s.
Mixed conifer	P	n.s.	P	n.s.
Lodgepole pine	N	n.s.	N	n.s.
Subalpine conifer	0.262	0.019	P	n.s.
Canopy cover index	0.374	0.001	P	n.s.
Large snag	0.426	<0.001	0.187	0.097
Small snag	0.265	0.018	P	n.s.
Small log	0.264	0.018	P	n.s.
Large log	0.400	<0.001	P	n.s.

TABLE 156. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and 3 measures of macrofungi genera richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Lichen richness	Fleshy fungi richness
<i>Channel characteristics:</i>		
Gradient	P	P
<i>Vegetation characteristics:</i>		
Subalpine conifer	P	-
Canopy cover index	P	-
Shrub	-	-
Large snag	P	P
<i>Variables in final model</i>		
adj. R^2	3 0.302	1 0.098

TABLE 157. Final regression model of key environmental variables related to lichen genus richness. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Canopy cover index	0.042	0.013	0.330	3.366	0.001
Large snags	1.236	0.381	0.317	3.241	0.002
Subalpine conifer	2.098	0.747	0.269	2.810	0.006

I looked for potential thresholds in lichen richness in relation to the 3 primary environmental variables associated with variation in richness. It appeared that ≥ 2 lichen genera

were consistently present on reaches where subalpine conifer was present (Fig. 61). Lichen genera richness was significantly greater in association with subalpine conifer (1-tailed test, pooled variance, $t = 2.43$, $P = 0.009$).

Lichen Richness by Basin Orientation

Lichen genus richness did not vary significantly by basin orientation based on ANOVA ($P = 0.826$).

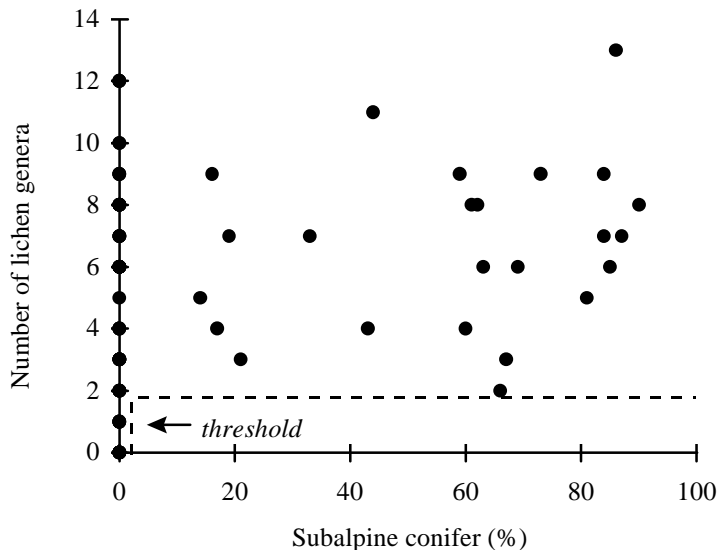


FIG. 61. threshold relationship between subalpine conifer and the richness of lichen genera. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of Fleshy Fungi Richness

Regression Model for Fleshy Fungi Richness

Fleshy fungi richness was correlated with only two variables: positive correlations with channel gradient and large snags (Table 155). Regression models reflected correlations (Table 156). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel variables resulted in a one-variable model: a positive association with channel gradient (adj. $R^2 = 0.098$). Regression on vegetation variables resulted in a weak one-variable model: positive association large snags (adj. $R^2 = 0.023$). Backwards step-wise regression on these 2 key variables resulted a weak one-variable model, where fleshy fungi richness increased with increases in channel gradient (adj. $R^2 = 0.098$, $B = 1.306$, SE of $B = 0.421$, Beta = 0.331, $t = 3.101$, $P = 0.003$) (Tables 156 and 157). No potential threshold was observed by examining the bivariate relationship between gradient and fleshy fungi richness.

Fleshy Fungi Richness by Basin Orientation

Fleshy fungi genus richness did not differ among basin orientations (ANOVA, $P = 0.584$).

Patterns of Fungi Rarity

General Patterns

Over 80% of all genera were present on < 25% of the reaches, with the remaining 10 genera ranging in frequency from 25 to 80% (Fig. 63). Approximately 78% of the genera (43 of 55) were present on less than 10% of the reaches. The average frequency of occurrence of rare genera was 2.2 reaches (SE = 0.28), and at least one rare genus was observed on 45.0 % ($n = 36$) of the reaches. Alternatively, the average frequency of occurrence of common genera was 24.1 reaches (SE = 3.19), and at least one common genus was observed on 95% ($n = 76$) of the reaches. The average number of rare genera per reach was 0.91 compared to an average of 6.34 common genera per reach (Table 158). Correlations between the number of rare and common genera per reach was high ($r = 0.405$, $P < 0.001$).

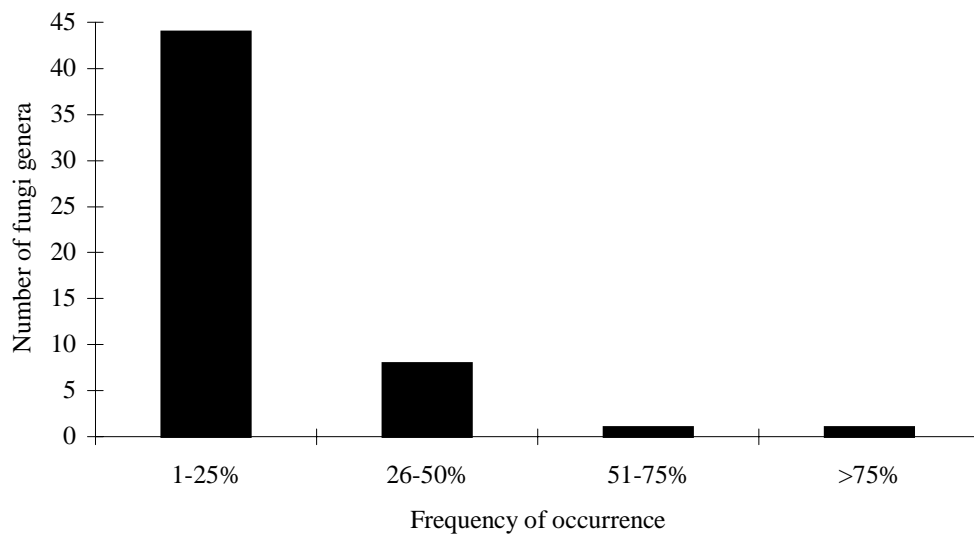


FIG. 62. Number of macrofungi genera occurring in each of 4 frequency of occurrence intervals. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

TABLE 158. Descriptive statistics for frequency classes for macrofungi genera. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Frequency class variable	Minimum	Maximum	Average	SE
Number of rare genera	0	6	0.91	0.16
Number of common genera	0	13	6.34	0.36

Environmental Relationships of Fungi Rarity

Correlations

Rare and common genera had different correlative relationships with 22 environmental variables (Table 159). Rare genera were correlated with few variables, including positive correlations with channel gradient and large snags. Common genera were correlated with many variables, including positive correlations with channel gradient, mixed conifer, canopy cover index, large snags, small logs, and large logs, and negative correlations with channel width, lodgepole pine, and meadow.

TABLE 159. Significant ($P \leq 0.10$) correlations between macrofungi rarity variables and environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Fungi rarity variables			
	Number of rare genera		Number of common genera	
	r	P	r	P
<i>Channel characteristics:</i>				
Gradient	0.301	0.007	0.529	<0.001
Width	N	n.s.	-0.202	0.072
<i>Vegetation characteristics:</i>				
Mixed conifer	P	n.s.	0.197	0.081
Lodgepole pine	N	n.s.	-0.239	0.033
Subalpine conifer	N	n.s.	0.263	0.018
Meadow	N	n.s.	-0.447	<0.001
Large snag	0.259	0.021	0.468	<0.001
Large log	P	n.s.	0.462	<0.001
Canopy cover index	P	n.s.	0.435	<0.001
Small logs	P	n.s.	0.309	0.005

Regression Model for Rare Fungi Richness

The number of rare genera was compared to environmental variables using multiple regression (Table 160). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel characteristics resulted in a one-variable model: a positive association with gradient (adj. $R^2 = 0.078$). Regression on vegetation characteristics resulted in a one-variable model: a positive association with large snags (adj. $R^2 = 0.055$). Backwards regression on these 2 key variables resulted in a weak 2-variable model, where rare fungi richness increased with increases in channel gradient and large snags (adj. $R^2 = 0.098$) (Tables 160 and 161).

TABLE 160. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and the number of genera in each of 2 macrofungi frequency classes. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Fungi rarity variable	
	Number of rare genera	Number of common genera
<i>Channel character:</i>		
Gradient	P	P
<i>Vegetation character:</i>		
Subalpine conifer	-	P
Large log	-	P
Large snag	P	-
Canopy cover index	-	P
<i>Variables in final model</i>	2	3
<i>adj. R²</i>	0.098	0.408

TABLE 161. Final backwards regression model of key environmental variables related to macrofungi rarity variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
<i>Number of rare fungi genera:</i>					
Channel gradient	0.300	0.183	0.184	1.640	0.105
Large snags	0.476	0.219	0.244	2.178	0.033
<i>Number of common fungi genera:</i>					
Gradient	1.238	0.465	0.275	2.661	0.010
Canopy cover index	0.037	0.012	0.301	3.153	0.002
Large logs	0.488	0.138	0.334	3.531	<0.001

Regression Model for Common Fungi Richness

The number of common genera was compared to environmental variables using multiple regression (Table 160). Regression on abiotic environmental variables resulted in no variables being selected. Regression on channel characteristics resulted in a one-variable model: a positive association with gradient (adj. $R^2 = 0.271$). Regression on vegetation variables resulted in a 3-variable model: positive relationships with canopy cover index, subalpine conifer, and large logs (adj. $R^2 = 0.388$). Backward regression on these 4 key variables resulted in a robust 3-variable model, where common genera richness increased with increases in channel gradient, canopy cover index, and large logs (adj. $R^2 = 0.408$) (Tables 160 and 161).

Fungi Rarity and Environmental Gradients

In general, rare and common genera richness had different relationships with environmental gradients (Table 162). The richness of common fungi genera was positively correlated with the elevation–precipitation and snag and log gradients, and negatively correlated with forest to

meadow, aspen–cottonwood, and channel flow gradients. The richness of rare fungi genera was only correlated with one gradient: a positive correlation with the snag and log gradient.

Fungi Rarity by Basin Orientation

The richness of rare and common fungi genera did not vary significantly among basin orientations (ANOVA, $P = 0.947$ and 0.437 , respectively).

TABLE 162. Correlations between macrofungi rarity variables and environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.10$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Number of rare genera		Number of common genera	
	r	P	r	P
<i>Physical gradient:</i>				
1. Elevation–precipitation	-0.123	0.279	0.198	0.079
2. Channel flow	0.037	0.747	-0.360	0.001
<i>Vegetation gradient:</i>				
1. Forest to meadow	-0.076	0.505	-0.399	<0.001
2. Subalpine vegetation	-0.052	0.644	0.176	0.119
3. Alder–willow	0.118	0.296	-0.044	0.698
4. Aspen–cottonwood	-0.159	0.159	-0.188	0.106
<i>Woody debris gradient:</i>				
1. Snag and log	0.213	0.058	0.497	<0.001

Patterns of Fungi Beta Diversity

Fungi Turnover Along Environmental Gradients

Genera Turnover

The lower of the gains and losses between any two segments represented the beta diversity for the 2 segments--the change in composition that was independent from alpha diversity. The sum of beta diversity across all 3 segment comparisons, “total turnover”, was used as the primary indication of the contribution of a gradient to beta diversity (Table 163). The precipitation gradient had the highest total turnover ($n = 28$), followed by aspen–cottonwood ($n = 22$), elevation ($n = 20$), elevation–precipitation ($n = 19$), and channel flow ($n = 19$) gradients. The snag and log gradient, as well as the subalpine vegetation gradient, had quite low turnovers ($n = 15$ and 12 , respectively).

TABLE 163. Beta diversity index values for macrofungi within and among 9 environmental gradients. The number of genera per segment, the number of genera only occurring at upper (“gains”) or lower (“losses”) ends of the gradient, and Whittaker’s beta diversity index (β_w) are displayed. A modified version of Whittaker’s beta diversity index (β_{wMIN}) is also displayed. Bolded values indicate turnover. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	β_w^*	β_{wMIN}^\dagger
<i>Elevation:</i>							
seg1:seg2	34	32	40	6	8	0.212	0.176
seg2:seg3	32	38	43	11	5	0.229	0.132
seg3:seg4	38	38	47	9	9	0.237	0.237
average							0.182
low:high	40	47	54	14	7	0.241	0.149
<i>Precipitation:</i>							
seg1:seg2	33	33	41	8	8	0.242	0.242
seg2:seg3	33	37	46	13	9	0.314	0.243
seg3:seg4	37	37	48	11	11	0.297	0.297
average							0.261
low:high	41	48	54	13	6	0.213	0.125
<i>Elevation–precipitation:</i>							
seg1:seg2	32	32	38	6	6	0.188	0.188
seg2:seg3	32	40	44	12	4	0.222	0.100
seg3:seg4	40	36	49	9	13	0.289	0.225
average							0.171
low:high	38	49	54	16	5	0.241	0.102
<i>Channel flow:</i>							
seg1:seg2	39	34	46	7	12	0.260	0.179
seg2:seg3	34	36	42	8	6	0.200	0.167
seg3:seg4	36	29	42	6	13	0.292	0.167
average							0.171
low:high	46	42	54	8	12	0.227	0.174
<i>Forest to meadow:</i>							
seg1:seg2	33	43	48	15	5	0.263	0.116
seg2:seg3	43	35	50	7	15	0.282	0.163
seg3:seg4	35	25	37	2	12	0.233	0.057
average							0.112
low:high	48	37	54	6	17	0.271	0.125
low:high	40	47	54	14	7	0.241	0.149

TABLE 163 cont.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	β_w^*	β_{wMIN}^\dagger
<i>Subalpine vegetation:</i>							
seg1:seg2	34	30	40	3	13	0.250	0.176
seg2:seg3	30	41	44	14	3	0.239	0.073
seg3:seg4	41	37	47	6	10	0.205	0.146
average							0.132
low:high	40	47	54	14	7	0.241	0.149
<i>Alder–willow:</i>							
seg1:seg2	38	34	46	8	12	0.278	0.211
seg2:seg3	34	33	42	8	9	0.254	0.235
seg3:seg4	33	36	42	9	6	0.217	0.167
average							0.204
low:high	46	42	54	8	12	0.227	0.174
<i>Aspen–cottonwood:</i>							
seg1:seg2	37	34	45	8	11	0.268	0.216
seg2:seg3	34	35	43	9	8	0.246	0.229
seg3:seg4	35	35	44	9	9	0.257	0.257
average							0.234
low:high	45	44	54	9	10	0.213	0.200
<i>Snag and log:</i>							
seg1:seg2	29	38	42	13	4	0.254	0.105
seg2:seg3	38	32	44	6	12	0.257	0.158
seg3:seg4	32	41	46	14	5	0.260	0.122
average							0.128
low:high	42	46	54	12	8	0.227	0.174

* Whittaker's beta diversity index: $S/\alpha - 1$, where S = total genera richness, and α = the average genera richness of the 2 segments being compared.

† Modified Whittaker's beta diversity index: $(S/s\text{-max}) - 1$, where S = total genera richness, and $s\text{-max}$ = the highest richness of the 2 segments being compared, resulting in a minimum beta diversity index value.

Patterns of turnover along each gradient provide additional insights as to their contributions to beta diversity based on presence (Table 163). Along the elevation, precipitation, and elevation–precipitation gradients, total richness increased from low to high segments, and turnover was greatest between the upper-most segments. Total richness was higher by 5 genera at the low end of the channel flow gradient, whereas turnover did not vary along the gradient. Along the forest to meadow gradient, total richness declined from the forest to the meadow end of the gradient, and turnover dropped to 2 genera between the upper-most segments. Total richness increased along the subalpine vegetation gradient, and turnover was also highest between the upper-most segments. Total richness and turnover did not vary greatly along the alder–willow gradient, with the low end of the gradient having 4 fewer genera and 2 more turnovers than the high end of the gradient. Along the aspen–cottonwood gradient, total richness and turnover varied

TABLE 164. Macrofungi genera present on 2 or more reaches and absent from lower or upper segments of each of 4 abiotic environmental gradient. Gradients were defined by principal components analysis. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin. All taxa had a frequency of occurrence of $\leq 10\%$.

Genus	Elevation gradient				Precipitation gradient				Elevation-precipitation gradient				Channel flow gradient			
	low < ----- > high				low < ----- > high				low < ----- > high				low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
<i>Frequency < 10%:</i>																
Tuckermannopsis		X							X							
Agaricus		X								X						
Sclerotinia			X								X					
Melanelia				X							X					
Collybia				X								X	X ₁			
Calvatia				X								X			X	
Aleuria					X					X			X			
Gyromitra							X									
Coprinus				X ₄				X				X ₄				X ₄
Calbovista												X				
Bryoria															X	
<i>Frequency $\geq 10\%$:</i>																
Noleana											X			X		
Tyromyces														X		
Summary	0	2	1	4	1	0	1	1	1	2	3	4	2	2	2	1

₁ Only occurs on segment 1.

₄ Only occurs on segment 4.

even less than along the alder–willow gradient, varying by only 1 to 2 genera. Total richness increased by 4 genera from low to high snag and log densities, and turnover was highest mid-gradient.

Whittaker's Index of Beta Diversity

The gradients were evaluated for their relative contribution to beta diversity in part based on a modified Whittaker's beta diversity index (β_{wMIN}), with the unmodified index value provided for comparison (Table 163). The average β_{wMIN} for segment comparisons along each gradient varied from a low of 0.112 for the forest to meadow gradient, to a high of 0.261 for the precipitation gradient. Next to precipitation, the aspen–cottonwood and alder–willow had the next highest β_{wMIN} values (0.234 and 0.204, respectively). The next set of 3 gradients had intermediate index values ranging from 0.171 to 0.182: elevation, elevation–precipitation, and channel flow. The 3 remaining gradients had much lower β_{wMIN} values.

Genera Presence

Genera contributing to gains and losses between lower and upper segments of each gradient were identified, along with genera showing additional trends of presence (absent from segment 1 or 4) along the gradient (Table 164 to 166). Genera specific associations with gradients indicate the relevance of the gradient to individual genera. Most genera had frequencies < 10%. Elevation and precipitation were analyzed separately, as well as their combined representation in the elevation–precipitation gradient (Table 165). Along the elevation gradient, none of the 7 genera restricted to lower elevation reaches were present on more than one reach. However, *Tuckermannopsis* (foliose lichen on conifers) and *Agaricus* (field mushrooms) were absent from the highest elevation reaches. Four of the 14 genera restricted to the upper elevation reaches were present on more than one reach: *Melanelia* (foliose lichen on rocks), *Collybia* (coincaps), *Calvatia* (puffball), and *Coprinus* (inky caps, restricted to highest elevation reaches). One genus was absent from the lowest elevation reach, *Sclerotinia* (a fleshy fungi). Very few genera turning over along the precipitation gradient were present on more than one reach. *Aleuria* (orange peel) was restricted to the lower end of the precipitation gradient, and *Coprinus* was restricted to the upper end of the gradient. The genera associated with the elevation–precipitation gradient were very similar to the patterns of association observed along the elevation gradient. One additional genus, *Calbovista* (giant puffball), was restricted to the upper end of the gradient. In addition, *Noleana* (a fleshy fungi) was absent from the lowest elevation–precipitation reaches, and it occurred on $\geq 10\%$ of the reaches.

Along the channel flow gradient, only 2 genera were restricted to low channel flow reaches, *Collybia* and *Aleuria* (Table 164). Two additional frequently occurring genera were absent from the highest channel flow reaches, *Noleana* and *Tyromyces*. Only one genus, *Coprinus*, was restricted to the highest channel flow reaches, with 2 additional genera were absent from the lowest channel flow reaches.

The snag and log gradient showed few turnovers in genera that occurred on more than one reach, and none were associated with genera present on $\geq 10\%$ of the reaches (Table 165). Only *Guepiniopsis* (alpine jelly cone) was restricted to the lower end of the gradient, with one additional genus, *Collybia*, being absent from the highest snag and log densities. A total of 3 genera were restricted to the upper end of the gradient: *Calbovista*, *Scutellinia*, and *Bisporella* (yellow fairy cup). Four additional genera were absent from the lowest snag and log density reaches. The higher number of genera restricted to the upper end of the gradient reflects the positive relationship between alpha diversity and snag and log densities.

TABLE 165. Macrofungi genera present on 2 or more reaches and absent from lower or upper segments of the snag and log gradient (derived by principal components analysis). All taxa had a frequency of occurrence of $\leq 10\%$. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Genus	Snag and log gradient			
	low < ----- >			
	high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
<i>Guepiniopsis</i>	X			
<i>Collybia</i>		X		
<i>Calvatia</i>			X	
<i>Melanelia</i>			X	
<i>Tuckermannopsis</i>			X	
<i>Agaricus</i>			X	
<i>Calbovista</i>				X ₄
<i>Scutellinia</i>				X ₄
<i>Bisporella</i>				X
<i>Dacrymyces</i>				
<i>Fomitopsis</i>				
<i>Gyromitra</i>				
<i>Summary</i>	1	1	4	3

₄ Only occurs on segment 4

Genera turnover was relatively high along vegetation gradients compared to the other gradients analyzed (Table 166). The forest to meadow gradient exhibited far more genera associated with the lower end of the gradient than the upper end, reflecting the positive relationship between fungi alpha diversity and forest vegetation. Only one genus was restricted to the meadow end of the gradient, *Coprinus*, with 2 additional genera absent from the most forested reaches (*Cladonia* and *Gyromitra*). In contrast, 6 genera were restricted to the forested end of the gradient. Four additional genera were absent from the upper most segment of the gradient, including *Tyromyces* and *Acarospora* which were present on $\geq 10\%$ of the reaches. A balanced number of genera were restricted to each end of the subalpine vegetation gradient. Two genera were restricted to the lower end of the gradient, *Calbovista* and *Fomitopsis*, and 3 genera were restricted to the upper end of the gradient, *Collybia*, *Coprinus*, and *Dacrymyces*. Two additional genera were absent from the lower most segment of the gradient. A balanced number of genera associated with each end of the gradient was also observed along the alder–willow gradient. Two genera were restricted to the lower end of the gradient, *Melanelia* and *Bryoria*, with one additional genus absent from the highest alder–willow density reaches, *Calvatia*. These genera may be averse to alder–willow vegetation. Conversely, two genera were restricted to the upper end of the alder–willow gradient, *Bisporella* and *Guepiniopsis*, with one additional genus absent from the lowest end of the gradient, *Tuckermannopsis*. Along the aspen–cottonwood gradient, only one genus was restricted to the lower end of the gradient, *Coprinus*, with one additional genus, *Melanelia*, absent from reaches with the highest proportion of aspen–cottonwood. Alternatively, the upper end of the gradient was uniquely associated with a few more genera than the lower end. Two genera were restricted to the upper end of the gradient, *Bisporella* and *Scutellinia*, with 3

TABLE 166. Macrofungi genera present on 2 or more reaches and absent from lower or upper segments of each of 4 vegetation gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Genus	Forest to meadow gradient low < ----- > high				Subalpine vegetation gradient low < ----- > high				Alder–willow gradient low < ----- > high				Aspen–cottonwood gradient low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
<i>Frequency < 10%:</i>																
Calbovista	X				X											
Fomitopsis	X				X											
Melanelia		X					X		X					X		
Tuckermannopsis	X						X				X				X	
Collybia								X								
Coprinus				X				X					X			
Dacrymyces								X								
Bryoria									X							
Calvatia										X						
Bisporella	X											X				X
Guepiniopsis												X				
Agaricus	X														X	
Cladonia			X												X	
Scutellinia	X															X
Aleuria		X														
Gyromitra			X													
<i>Frequency ≥ 10%:</i>																
Tyromyces		X														
Acarospora		X														
<i>Summary</i>	6	4	2	1	2	0	2	3	2	1	1	2	1	1	3	2

₁ Only occurs on segment 1.

₄ Only occurs on segment 4.

additional genera absent from the lower most segments along the aspen–cottonwood gradient: *Tuckermannopsis*, *Agaricus*, and *Cladonia*.

Ranking Gradients for Beta Diversity

The 8 environmental gradients were ranked to reflect their contribution to beta diversity based on genus presence data (Table 167). The precipitation gradient ranked highest in total turnover and had the highest Whittaker's index, followed by aspen–cottonwood and alder–willow. The next 2 gradients were close in turnover, with elevation being slightly greater than channel flow. The remaining 3 gradients had substantially lower total turnover. Forest to meadow ranked second to last in terms of total turnover, but by far had the highest core turnover of any gradient. The combined elevation–precipitation gradient was not ranked in Table 167 because it was redundant with the individual elevation and precipitation gradients, however as a point of comparison it would have ranked 6th, just below channel flow (total turnover = 19, core turnover = 10, $\beta_{wMIN} = 0.171$). The combination of elevation and precipitation appeared to mask the individual contributions of elevation and precipitation to the beta diversity of fungi.

TABLE 167. Ranking of environmental gradients by their contribution to macrofungi beta diversity based on presence in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Total turnover	Core turnover - freq. ≥ 2 reaches	Average β_{wMIN}	Rank
Precipitation	28	3	0.261	1
Aspen–cottonwood	25	7	0.234	2
Alder–willow	22	6	0.204	3
Elevation	20	7	0.182	4
Channel flow	19	7	0.171	5
Snag and log	15	9	0.128	6
Forest to meadow	14	13	0.112	7
Subalpine vegetation	12	7	0.132	8

Fungi Turnover by Basin Orientation

Basin orientation can affect genus turnover, as did the environmental gradients analyzed above. All pair-wise comparisons of orientations were conducted to assess the contribution of basin orientation to genera turnover (Table 168). Based on the average β_{wMIN} across all orientation comparisons, orientation had a similar range of values in genus turnover and an intermediate beta diversity index. The greatest genera turnover, as well as the greatest balance between gains and losses and the highest β_{wMIN} value, occurred between the east and south orientations ($n = 9$). The lowest turnover occurred between east and west orientations. It was not possible to compare patterns of genus turnover between basin orientation and the other gradients because orientations can not be aligned along a linear gradient. However, comparison of east–dry and west–wet orientations provides a representation of all orientation comparisons. The genus turnover between these 2 halves of the basin was moderate (genus turnover = 7, genera turning over with frequency $\geq 4 = 1$, $\beta_{wMIN} = 0.198$) compared to the other gradients, placing approximately between high turnover vegetation gradients and the elevation and precipitation gradients in terms of contributions to beta diversity.

TABLE 168. Beta diversity index values for macrofungi among basin orientations. The number of genera per segment, the number of genera only occurring at upper (“gains”) or lower (“losses”) ends of the gradient, and Whittaker’s beta diversity index (β_w) are displayed. A modified version of Whittaker’s beta diversity index (β_{wMIN}) is also displayed. N = north, E = east, S = south, W = west side of the basin. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Basin orientation	Richness of first segment	Richness of second segment	Total richness	Gains	Losses	β_w^*	β_{wMIN}^\dagger
N:E	35	33	42	7	9	0.235	0.200
E:S	33	32	42	9	10	0.292	0.273
S:W	32	39	47	15	8	0.394	0.205
N:S	35	32	42	7	10	0.254	0.200
E:W	33	39	44	11	5	0.222	0.128
N:W	35	39	46	11	7	0.243	0.180
<i>average</i>							<i>0.198</i>
<i>N and E:S and W</i>	<i>42</i>	<i>47</i>	<i>54</i>	<i>12</i>	<i>7</i>	<i>0.213</i>	<i>0.149</i>

* Whittaker’s beta diversity index: $S/\alpha - 1$, where S = total genera richness, and α = the average genera richness of the two segments being compared.

† Modified Whittaker’s beta diversity index: $(S/s\text{-max}) - 1$, where S = total genera richness, and $s\text{-max}$ = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

Seventeen genera (31.5%) were absent from one or more orientations (Table 169), with 6 of these genera having frequencies $\geq 10\%$. Only one genus was unique to one orientation; *Bisporella* occurred only on the west side of the basin, grows on dead twigs and branches (Lincoff 1981), and may be restricted to moister environments in the basin. The greatest number of genera ($n = 11$) were absent from the south side of the basin, with the west side having the least number of genera absent ($n = 4$). No genera were absent only from the north side of the basin, but 2 genera were absent only from the xeric east side of the basin, *Gyromitra* (false morel) and *Agaricus* (field mushrooms), both of which are fleshy fungi with frequencies $\geq 10\%$ and which grow on soil (McKnight and McKnight 1987). They may be most vulnerable to dry conditions because of their association with soil substrates. An additional fleshy fungi genus, *Coprinus* (inky caps), was absent from both the north and east sides of the basin. These genera represent the genera most likely to be moisture limited in the basin. Three genera were absent from the south side of the basin: *Tyromyces* (a polypore), *Acarospora* (crustose lichen), and *Cladonia* (fruticose lichen), all of which have frequencies $\geq 10\%$. Only one lichen genus, *Melania* (foliose lichen), was absent from the west side of the basin. One additional fleshy fungi genus, *Aleuria* (orange peel), was absent from the south and west sides of the basin.

TABLE 169. Macrofungi genera present on 2 or more reaches and absent from one or more basin orientations. X's indicate where genus was present. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Genus	Type	Presence by basin orientation			
		Xeric < ----- > Mesic			
		North side	East side	South side	West side
<i>Frequency < 10%:</i>					
Bisporella	Fleshy				X
Calbovista	Fleshy		X		X
Sclerotina	Fleshy		X	X	
Scutellinia	Fleshy		X		X
Tuckermannopsis	Lichen		X		X
Coprinus	Fleshy			X	X
Fomitopsis	Fleshy		X		X
Collybia	Fleshy	X			X
Dacrymyces	Fleshy	X			X
Guepiniopsis	Fleshy	X		X	
Melanelia	Lichen	X	X	X	
<i>Frequency ≥ 10%:</i>					
Gyromitra	Fleshy	X		X	X
Agaricus	Fleshy	X		X	X
Tyromyces	Fleshy	X	X		X
Acarospora	Lichen	X	X		X
Cladonia	Lichen	X	X		X
Aleuria	Fleshy	X	X		
<i>Sum of absent genera</i>		7	7	11	4

Concordance Between Diversity Measures

Measures of Alpha Diversity

Most correlations between diversity measures were positive and significant, with the only exception being the lack of correlation of rare genera and lichen genera (Table 170). The strongest correlations were between common genera richness and both lichen genera richness and total fungi genera richness, indicating that patterns of genera richness were driven by common lichen genera. Rare genera and fleshy fungi genera were also highly correlated, suggesting that most fleshy fungi were rare. Rare and common genera were not highly correlated, suggesting that rare genera had some unique patterns of association compared to common genera.

TABLE 170. Correlations among measures of macrofungi alpha diversity. Bolded values indicate $P \leq 0.05$. Shading indicates redundant cells. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Fungi diversity variables	Total fungi richness		Rare genera richness		Common genera richness		Lichen genera richness	
	r	P	r	P	r	P	r	P
Rare genera richness	0.676	<0.001						
Common genera richness	0.948	<0.001	0.405	<0.001				
Lichen genera richness	0.754	<0.001	0.171	0.129	0.861	<0.001		
Fleshy fungi genera richness	0.557	<0.001	0.807	<0.001	0.341	0.002	-0.122	0.282

Alpha and Beta Diversity

An average of 32.8 (range = 25 to 38, SE = 0.58) fungi genera were shared among segments ($n = 20$ reaches per segment), based on segment comparisons across all 8 environmental gradients. The average richness lost or gained between segments was 4.8 genera (range = 0 to 11, SE = 0.76), and it was not significantly different (based on paired t-test across gradients, $t = 1.44$, $P = 0.166$) than the average number of genus turnovers between segments ($\bar{x} = 6.5$ genera, range = 2 to 11, SE = 0.45). The average number of genera shared among segments constituted 59.6% of all genera observed, and variation in richness and genera turnover constituted 8.7% and 11.8%, respectively, of all genera observed.

The analysis of the relative influence of environmental gradients on gamma diversity in the basin showed that the precipitation gradient had the greatest contribution to gamma diversity in the basin (Fig. 64). The precipitation gradient showed a shift in 32 genera along its length, comprising approximately 59% of the total fungal fauna. The diversity associated with the precipitation gradient was primarily driven by genus turnover. The precipitation gradient was followed in the magnitude of its contribution to gamma diversity by the channel flow gradient, which showed a shift in 29 genera along its length and contributions from both alpha and beta diversity. The aspen–cottonwood and snag and log gradients both showed a shift of 27 genera along their lengths, with the snag and log gradient having a balanced contribution from alpha and beta diversity, whereas diversity associated with the aspen–cottonwood gradient was dominated by beta diversity. The remaining gradients had lower contributions to gamma diversity. The difference in compositional change among the gradients ranged as high as 17 genera—over 30% of the observed total richness.

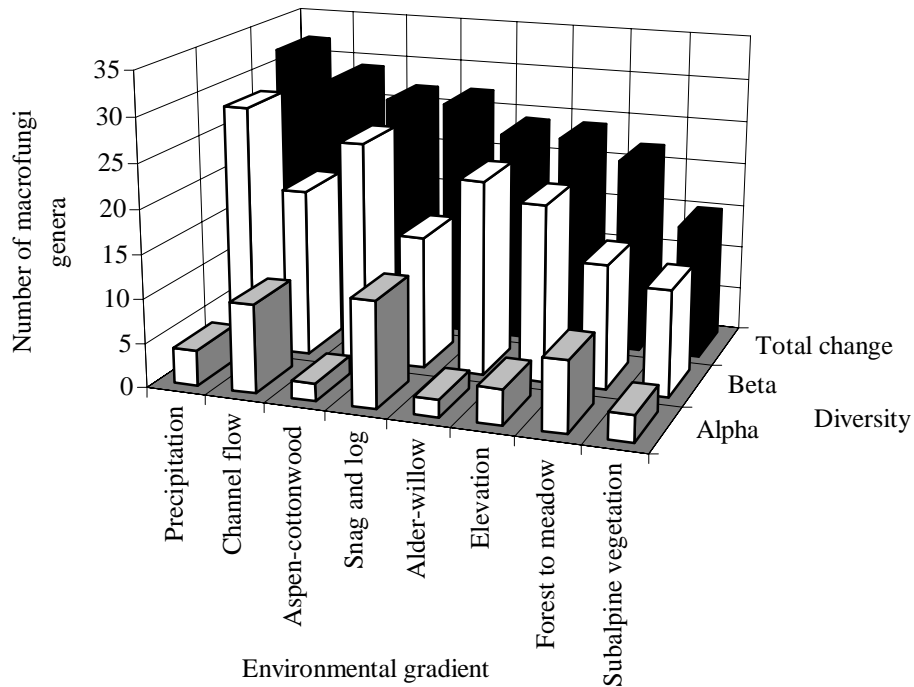


FIG. 63. Contribution of each of 8 environmental gradients to macrofungi diversity of the Lake Tahoe basin. Total change in composition is shown, along with the composite contributions of alpha and beta diversity. Data were collected on 80 sample reaches in 1995 and 1996.

The total change in composition was more closely correlated with beta diversity ($r = 0.743$, $P = 0.035$) than alpha diversity ($r = 0.260$, $P = 0.533$), and the individual contributions of alpha and beta diversity were not correlated ($r = -0.453$, $P = 0.259$). In general, net changes in richness (alpha diversity) along gradients were lower but more variable than changes in composition (beta diversity).

DISCUSSION

Environmental Influences on Macrofungi Diversity

I encountered a relatively low number ($n = 55$) of fungi genera, compared to the number of genera Manley et al. (2000) identified as potentially occurring in the Lake Tahoe basin ($n = 339$). However, the estimates of Manley et al. (2000) are highly inclusive (including genera occurring across the Sierra Nevada) and are likely to be overestimates. The number of documented fungi genera in Manley et al. (2000) total only 60 genera, and thus my sample represents over 90% of all fungi genera known to occur in the basin.

Reaches ranged widely in environmental conditions, resulting in richness and turnover making similar magnitude contributions to the diversity of fungi basin-wide. Each reach contained an average of 13% and as high as 29% of the total number of fungi genera observed throughout the Lake Tahoe basin. Similarly, turnover was moderate, averaging 13% and ranging from 9% to 16% of all genera between the lower to upper halves of the 8 environmental gradients examined. Therefore, environmental features that influenced either richness or turnover were

important in determining fungi diversity in the Lake Tahoe basin.

Lichen genera were the predominant fungi life form encountered in my study. The seasonal nature of fruiting-bodies of fleshy fungi made them less detectable than lichen genera, which are physically present all year long. The result was that even though I encountered more fleshy fungi genera than lichen genera, lichen genera were detected on twice as many reaches and the average frequency of occurrence was over 3 times higher compared to fleshy fungi. Thus, lichen genera, because of their high frequency of occurrence, formed the base composition of genera across most reaches.

Richness and turnover were driven by different environmental features and generally varied in opposition to one another. Richness was primarily associated with channel flow characteristics and coniferous vegetation, whereas turnover was primarily associated with precipitation and riparian woodland vegetation. The opposing relationships of richness and turnover are most likely a reflection of the different environmental relationships of lichen and fleshy fungi, where lichen dominated patterns of richness, and fleshy fungi was primarily responsible for turnover between reaches and gradient segments. Thus, the strong upland vegetation associations of lichen and the most common fleshy fungi (i.e., *Polypore*, *Cryptoporus*, and *Hemitricia*) were expressed in the environmental relationships of most measures of richness (specifically, lichen, common fungi, total fungi richness), and the moisture-related environmental sensitivities and relationships of fleshy fungi were reflected in the gradients associated with turnover.

Environmental features were strongly associated with variation in fungi diversity. For example, environmental variables were able to explain from 30.2% for lichen richness, to 38.5% for total fungi richness, to 40.8% for common genera richness. Abiotic environmental features had the greatest overall influence on the diversity of fungi genera, with vegetation types having a strong secondary effect. The precipitation gradient showed the greatest contribution to diversity, which was primarily a consequence of high genus turnover. The high turnover along the precipitation gradient suggests that genera were somewhat specialized along the precipitation gradient and that turnover was driven by rare genera. No genera with frequencies $\geq 10\%$ and no unique genera were absent along the precipitation gradient. Richness and turnover were low in association with elevation; however, when combined with precipitation in the elevation-precipitation gradient, a positive association with richness (total and common genera) was observed.

The channel flow gradient was the second highest contributor to fungi diversity in the Lake Tahoe basin, and was the only gradient associated with both richness and turnover. Turnover was consistent along the channel flow gradient, ranging from 6 to 7 genera between segments, and it appeared that more frequent genera (present on 2 or more reaches) were absent from the more extreme channel flow conditions. Richness was negatively associated with channel flow, with channel gradient as the primary influence. The pervasive positive influence of channel gradient on richness indicates that fungi genera are more diverse in upland environments than riparian environments, particularly common genera.

Fungi genera richness was negatively correlated with meadow and lodgepole pine and positively correlated with mixed conifer and logs. The forest to meadow gradient was highly correlated with the channel flow gradient ($r = 0.449$, $P < 0.001$), and its association with diversity essentially indicates that areas of higher channel flow have broader floodplains and more meadow, and lower channel flow reaches are more dominated by upland forested conditions. Although the forest to meadow gradient ranked low in turnover, it had the highest number of core turnovers (genera present on more than 1 reach) among segments ($n = 13$ genera), and over 7% were associated with genera not occurring in upper segments (meadow–lodgepole pine portion) of the forest to meadow gradient. One genus, *Coprinus* (inky caps), only occurred

in the meadow–lodgepole pine portion of the gradient.

The aspen–cottonwood gradient was the third greatest contributor to the diversity of fungi genera in the Lake Tahoe basin. Most of the diversity associated with the aspen–cottonwood gradient was contributed by turnover, as was observed for the precipitation gradient. Thus, aspen–cottonwood provides a specialized environment for fungi, particularly fleshy fungi. Specifically, fleshy fungi genera *Scutellinia* (eyelash pixie cup) and *Bisporella* (fairy cups) were absent from the lower half of the aspen–cottonwood gradient.

A variety of environmental variables associated with higher elevation conifer forests were positively associated with the richness of lichen and common genera (consisting primarily of conifer-associated lichen and fleshy fungi). The snag and log gradient was unique among all gradients in that it was strongly positively associated with the richness of both rare and common fungi. These results indicate that snags and logs serve as an important substrate for both lichen and fleshy fungi. Subalpine conifer ranked last in its contribution to fungi diversity in the Lake Tahoe basin, but the richness of lichen and common fungi were significantly positively correlated with subalpine vegetation. Finally, canopy cover was also positively associated with the richness of these same 2 fungi groups.

The alder–willow gradient was associated with relatively high turnover (3rd highest gradient), but was not associated with richness and thus overall had a relatively limited influence on diversity. As observed along the aspen–cottonwood gradient, alder–willow appears to provide a specialized environment for some fungi genera. Specifically, fleshy fungi genera *Bisporella* and *Guepiniopsis* were restricted to the upper half of the alder–willow gradient.

Individual Genera and Genera Groups

Genera groups were valuable in discerning finer patterns of environmental influence on richness. It was obvious that the most commonly occurring genera dominated the environmental relationships exhibited by total fungi richness. The investigation of fleshy fungi and lichen richness revealed that rare genera were dominated by fleshy fungi and common genera were dominated by lichen genera. Thus, the environmental relationships of fleshy fungi and lichen were reflected in the environmental relationships of rare and common genera, respectively.

The richness of fleshy fungi was not strongly related to the environmental conditions described in this study (< 10% of the variation in richness explained). The lack of a relationship between environmental variables and fleshy fungi is most likely a reflection of the relatively high number of fleshy fungi genera combined with their relatively low frequency of occurrence, resulting in a constantly shifting assemblage of fleshy fungi among reaches. Alternatively, environmental variables described 30% to 40% of the variation in lichen and common genera richness. Lichen richness was strongly associated with conifer vegetation.

Three genera occurring on $\geq 10\%$ of the reaches were restricted to a portion of one or more environmental gradients, and may be reaching environmental limits along the associated gradients. *Tyromyces* was absent from the highest channel flow segment and the lower most segment of the forest to meadow gradient. *Tyromyces* is a fleshy fungi that attacks dead or dying conifers trees (Arora 1986). *Noleana* was absent from the highest channel flow segment and from the lowest segment of the elevation–precipitation gradient. *Noleana* is saprophytic, growing on the ground or woody debris (Lincoff and Nehring 1981, Arora 1986), and it is most likely limited by the availability of woody material. *Acarospora*, like *Tyromyces*, was absent from the lower-most segment of the forest to meadow gradient. *Acarospora* is a wide-spread crustose lichen genus occurring primarily on exposed acidic rocks in sunny locations at high elevations (Hale and Cole 1988). Rocks are far less common in meadows compared to forested environments in the Lake Tahoe basin, and so the lack of available of rocky substrates is most

likely to be the reason for its absence from meadows.

Conservation and Management Implications

Few studies have investigated turnover in fungi along environmental gradients (e.g., McCune and Antos 1981, Pharo et al. 1999). My study showed that fungi richness in the Lake Tahoe basin was associated with multiple environmental gradients. It appeared that the rarest of genera, primarily fleshy fungi, were responsible for the high turnover observed along the precipitation gradient. Fleshy fungi fruiting bodies typically require moist environments (Arora 1986), which would potentially lead to a greater richness of fungi in association with increases in precipitation, but lower richness at higher elevations because of lower temperatures. Thus fleshy fungi responded strongly to the 150 cm precipitation gradient in the basin.

Conifer forests were the environment where fungi richness and turnover was greatest. The greatest potential management effects on fungi diversity are from timber harvest and fire management. Timber harvest activities could reduce suitable live and dead trees substrates, and invoke frequencies of disturbance that reduce the ability for fruiticose and foliose lichen to persist and grow. Fire could pose threats to lichen diversity if uncharacteristically large and hot fires occurred, as opposed to a more natural fire regime consisting of more frequent, less intensive fires.

Subalpine conifer, a high elevation vegetation type, was positively associated with fungi richness. Lichen diversity commonly increases in association with elevation (e.g., Dietrich and Scheidegger 1997), as observed in my study. Further, lichen are able to survive in drier habitats than other fungi, but they draw most of their water and nutrients from the atmosphere, and therefore are metabolically active only when moist (Hudson 1986). Thus, lichen can tolerate a range of moisture regimes (Hudson 1986), but their diversity is commonly positively associated with precipitation (Hale and Cole 1981), which increased with elevation in the Lake Tahoe basin. The positive relationship observed between lichen richness and subalpine conifer probably reflects a high prevalence of both conifers and rocky substrates, the primary substrates of lichens encountered in the study area. Thus, it appears that common patterns of association between lichen and elevation were observed along the 1000 m elevation gradient occurring within the basin.

The close association between rare genera, namely fleshy fungi, and both aspen–cottonwood and alder–willow points toward important considerations the management of aspen and cottonwood stands. The genera restricted to the upper ends of the aspen–cottonwood and alder–willow gradients may be moisture limited, and management the may affect the moisture regime in riparian woodlands could negatively affect fungi diversity in the Lake Tahoe basin. For example, aspen stands are sometimes ephemeral vegetation associations which are succeeded by conifer forests in the absence of fire. However, depending on soils and moisture, some aspen stands can be relatively permanent features even in the absence of fire (Barry 1971, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin. A mosaic of aspen–cottonwood intermixed with conifer vegetation types would support the greatest diversity of fungi in the basin.

Alder and willow occurred frequently along stream reaches, and was generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, however grazing and channel restoration could alter its abundance. Channel restoration could affect alder and willow abundance, as well as meadow conditions. Restoration efforts that involve key meadow complexes with well developed alder

and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow habitat.

Most of the lichen and fleshy fungi genera detected in my study are associated with woody materials, living or dead, and fungi richness was bolstered by snags and logs, given that many fleshy fungi are associated with dead wood substrates. Large logs were strongly associated with all measures of fungi diversity, with richness being greater at higher densities of large logs. It is likely that the relationship between richness and the snag and log gradient is a reflection of this relationship. Most of the fungi genera were associated with dead wood, and it is apparent that logs play an important role in supporting a diversity of fungi in the Lake Tahoe basin. A high density of small snags and logs occur in the basin as a result of recent large-scale tree mortality events (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), as evidenced by the high frequency of occurrence (> 80%) of large snags and both sizes of logs across all sample reaches. Management of snags and logs to benefit fungi diversity should focus on the retention and recruitment of large snags and logs. Future attempts to reduce fine fuels in the Lake Tahoe basin (Manley et al. 2000) may also pose a risk to the quality and quantity of large snags and logs as substrates for fungi. Careful fire management to conserve values provided by large snags and logs would contribute to retaining substrates for fungi.

No relationships were observed between richness and orientation within the Lake Tahoe basin. This is consistent with the lack of observed relationships between fungi diversity and the physical features described in this study. It is likely that fungi richness is responding to finer scale features in the environment, such as snags and logs, which do not vary substantially by basin orientation. Therefore, the distribution of management activities around the basin does not appear to be a major consideration in the conservation of fungi diversity in the basin.